

## **Dynamics of a population of burrowing wolf spiders. Is there any competition?**

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**Dynamics of a population of burrowing wolf spiders. Is there any competition?** - Population dynamics of the wolf spider *Lycosa tarentula fasciiventris* (Dufour, 1835) (Araneae, Lycosidae) has been studied for almost a complete year. The distribution patterns of the burrows and the developmental stage, sex, prosoma and patella-tibia length of the burrow occupants were collected fortnightly during that period. Individuals were marked after each moult. *L. tarentula* seems to be a biannual and iteroparous species. There were peaks in burrow recruitment of the one-year-old juveniles in September (after the spiderlings hatched) and in August (after the adult males leave their burrows searching for mates). These recruitment periods can be explained by a lack of competition. The juveniles, after occupying a burrow, can either stay inside until adulthood or leave it. We present a preliminary Cox proportional hazards regression model, showing a pattern of density-dependent burrow leaving for juveniles. Interference competition for burrow-sites could play a role in population regulation.

**Key-words:** *Lycosa tarentula fasciiventris* - burrowing wolf spiders - population dynamics - Thiessen polygons - interference competition - burrow-site

### **INTRODUCTION**

The role of competition for food resources in spiders is a problem not yet completely solved by ecologists (WISE 1993). Web-building spiders have been well studied, whereas in wandering spiders, the first evidence of the existence of exploitative competition was found few years ago in an experiment with *Schizocosa ocreata* (Hentz) (WISE & WAGNER 1992).

Competition by territorial interference has been successfully studied in the field with *Agelenopsis aperta* (Gertsch), a sheet web spider (RIECHERT 1981, 1982), but in wandering spiders there is little field evidence that this pattern is happening. We found indirect evidence for the existence of interference competition in burrowing lycosids. This is based on phenological data and spatial distribution in a population of *Lycosa tarentula fasciiventris* (Dufour, 1835). We discuss the possible role of such a competition in the study population, taking as a basis field data and a preliminary model based on Cox proportional hazards regression (COX 1972, MUENCHOW 1986).

## MATERIAL AND METHODS

The study was carried out in the "Parc Natural del Massís de Garraf", in South of Barcelona. The area is a maquis (typically Mediterranean shrub vegetation community, 0.5–2 m in height) of kermes oak (*Quercus coccifera* L.) and Pistachio (*Pistacia lentiscus* L.) with a dominance of the former.

A plot of 540 m<sup>2</sup> was defined and all burrows monitored fortnightly (from late August 1992 to August 1993). At each visit, Cartesian co-ordinates of the new burrows were measured, the burrowers were extracted, and the prosoma width and length, and the patella + tibia length of their right foreleg were measured. The developmental stage of each spider was recorded on every occasion (juvenile, male, subadult male, female or subadult female). The animals were extracted by inserting a thin wire in the burrow's mouth and shaking gently. When this was done, the spider left the burrow suddenly, and could be collected in a vial. They were measured in a small mesh bag and marked on the legs with enamel. The mark was replaced after moulting. Then each individual was released into the burrow using a funnel. A colour code was used to identify every individual for monitoring until the next moult.

The study species needs almost two years to reach adulthood (FERNANDEZ-MONTRAVETA *et al.* 1991, ORTA *et al.* 1993), and females can reproduce both in that year and in the next (ORTA *et al.* 1993) like other species (MCQUEEN 1978). In this way, generations overlap and 4 cohorts can co-occur in October (recently dispersed spiderlings, one-year-old juveniles, first-year reproductive females and second-year reproductive females). Contrary to what happens in other populations of this species (e.g. FERNANDEZ-MONTRAVETA *et al.* 1991), most juveniles do not establish themselves until they are one year old or more. Two burrows of juveniles less than one year old were detected, and they were not included in this analysis. The cohort of one-year-old juvenile burrowers has been studied in more detail. Data on population dynamics refer only to burrowers.

### A preliminary model to test the possible existence of interference competition

With the present model we sought to disentangle the variables that could determine the time that one-year-old juveniles remained in their burrows, since the abandonment rate was quite high (fig. 3). We developed a preliminary model based on Cox proportional hazards regression (COX 1972, MUENCHOW 1986) to see what

variables influence the residence time of young spiders. The dependent variable in survival analysis is "time until an event occurs". In this case, the event was "to leave the burrow". We assumed that the site tenacity of each individual was influenced by their nearest neighbours. The neighbours considered were the ones that shared Thiessen polygon boundaries longer than 50 cm with the focal individual, because they would have a high probability of encounter with the later (arrows in figure 1 show the nearest neighbours of individual A as an example). While focal individuals were only one-year-old juveniles, 'potential influencing neighbours' included first year reproductive females as well. Second year reproductive females were discarded: we expected a weak influence of these females upon juvenile burrowers since by the time the data were collected they were too old and died during the winter.

We used two independent variables in the model:

- $Q_t$  - Ratio between the prosoma length of the focal individual and the average prosoma length of their neighbours in the date of sample  $t$ . This ratio indicates the size of the focal individual relative to its neighbours. So, it is an index of the probability of win in an encounter with other territory holders. For each animal, the mean of this index ( $\bar{Q}$ ) among all the sample dates in which it was present was used. This is because neighbour individuals can change across dates, due to the high rate of leaving burrows.
- $A_t$  - The area of the Thiessen polygon of the focal individual at the sample date  $t$ . This area can be considered the potential territory of each individual (DIGGLE 1983, KENKEL *et al.* 1989). To avoid edge effects, we have considered it convenient not to eliminate the polygons partially bounded with an edge of the study area, nor any interior polygons (KENKEL *et al.* 1989), because the sample would be enormously reduced. In order to counteract this error and to adjust the model to the real spatial heterogeneity, we have eliminated in each Thiessen polygon the potentially non defensible area; that is, the area occupied by bushes and rocks, where no spider could place its burrow (BARRIENTOS *et al.* 1994) (fig. 1). To draw this area, a grid of 3x3 m was built in the field and all the elements where we expected the spider would not place the burrow were drawn. The elements with a diameter smaller than 25 cm were discarded. This area was drawn a year before the study, and their suitability for burrow settlement demonstrated a year later (BARRIENTOS *et al.* 1994). In figure 1 we see the theoretically available area corresponds quite neatly with the area occupied by the burrows of the present study. To subtract and recalculate the exclusion area from the available one we have used the IDRISI package. We used the mean of the index among sample dates ( $\bar{A}$ ), as in the above variable.

The dependent variable ('time until the focal individual leaves the burrow') was measured as the sum of fortnightly time intervals when the animal was present (discrete case of Cox proportional hazards regression). The criterion to decide whether or not the burrow were abandoned, was the failure of spider extraction in consecutive sample dates, and the previous evidence that burrow maintenance (that is

to clean the burrow's mouth) had been stopped by the spider; rubbish that fell down the burrow had not been removed.

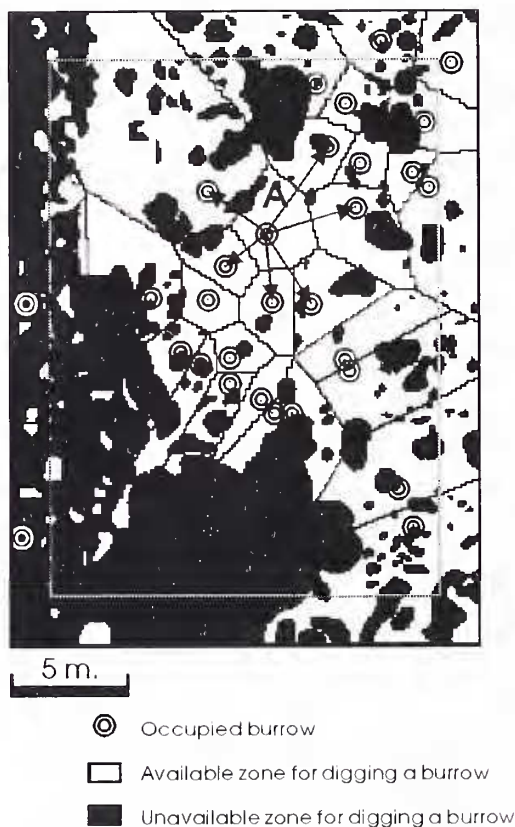


FIG. 1

Map of the study plot. The internal frame shows the area considered avoiding edge effects when calculating the nearest neighbour distances. In black is the area unavailable for burrow placement (shrubs and rocks) and discarded in the calculations of Thiessen polygon areas, in white the available area. Focal individual A is used as an example to explain the two independent variables in the Cox regression model (see text).

The theoretical model of proportional hazards is as follows:

$$h(t, \bar{Q}, A) = h_0(t) \exp(\beta_1 \bar{Q} + \beta_2 A)$$

Where  $\beta_1$  and  $\beta_2$  are coefficients of  $\bar{Q}$  and  $A$  respectively and  $h_0(t)$  is an unknown initial hazard function of each individual. A Chi-square test (log-likelihood method) was used to fit this model.

### Nearest neighbour distance

We have applied the method of nearest neighbour distances (CLARK & EVANS 1954) to the spatial plots of almost all the sampling dates, to see if the distributions are as regular as we would expect in a territorial system (DAVIES 1978, BURGESS & UETZ 1982). To minimise the edge effects (SINCLAIR 1985), we have not considered as focal individuals the ones within an area of 2 m from the edge (fig. 1). This analysis includes as focal individuals all the animals that occupied a burrow (adults and juveniles). A simple program in C language, working with Euclidean distances from the Cartesian coordinates of the burrows, has been implemented for calculations (BURGESS & UETZ 1982). To calculate the expected distances, the total area of the plot should be used, but, since the suitable habitat seems to be restricted (BARRIENTOS *et al.* 1994), we decided to calculate the expected distances considering only the available area within the subplot resulted after subtracting the 2 m edges (173 m<sup>2</sup>, fig. 1). As an indirect evidence of territoriality (DAVIES 1978), we expected to find a regular distribution within such area.

## RESULTS

### Burrow Occupation Dynamics

There were two periods of burrow settlement during the study (fig. 2 and fig. 3). The first one appeared in September, just when the spiderlings were hatched and were on top of their mother (ORTA *et al.* 1993). The second appeared in early August, just after the adult males left their burrows (fig. 3). The individuals that established their burrows in September–October were used in the Cox model, and they became adults in June. The spiders that set up the burrows in August were a later cohort found in the last sampling date, so no monitoring was established for them. The failure of juvenile burrowers before the reproductive season (June) was followed by a similar rate of recruitment (fig. 3).

### Fitting the Model

To make the model fit we have included the sampling dates from September 1992 to the beginning of June 1993, when the males reached maturity and left their burrows searching for mates, and became impossible to monitor. The result is:

$$h(t, Q, A) = h_0(t) \exp(-2.08\bar{Q} + 0.07\bar{A})$$

(Chi-square  $\chi^2 = 11.4$ , 2 d.f.,  $p < 0.005$ ,  $n = 61$ ). The value of  $\beta_1$  is negative, indicating that the smaller the focal individual was relative to their neighbours, the higher the probability of abandoning its burrow. The value of  $\beta_2$  is positive, so the larger the potential territory of the focal individual, the higher the probability of abandoning its burrow.

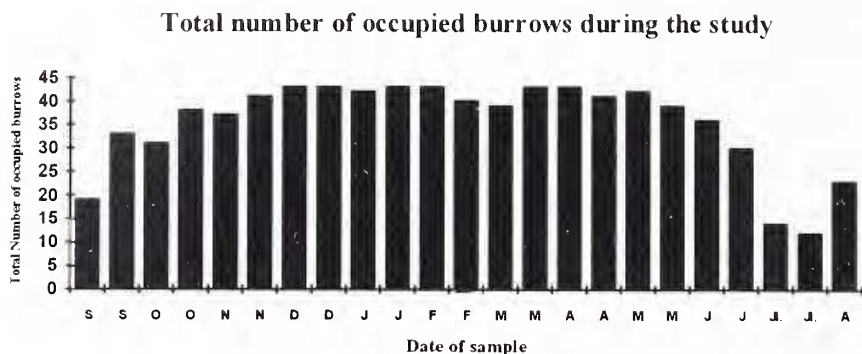


FIG. 2

Total number of occupied burrows in each sample date (1992–1993). There were new entries of one-year-old juveniles in September and in August. The decrease of burrowers in July was when all the juvenile burrowers reached adulthood and the males left their burrows searching for females (see also fig. 3).

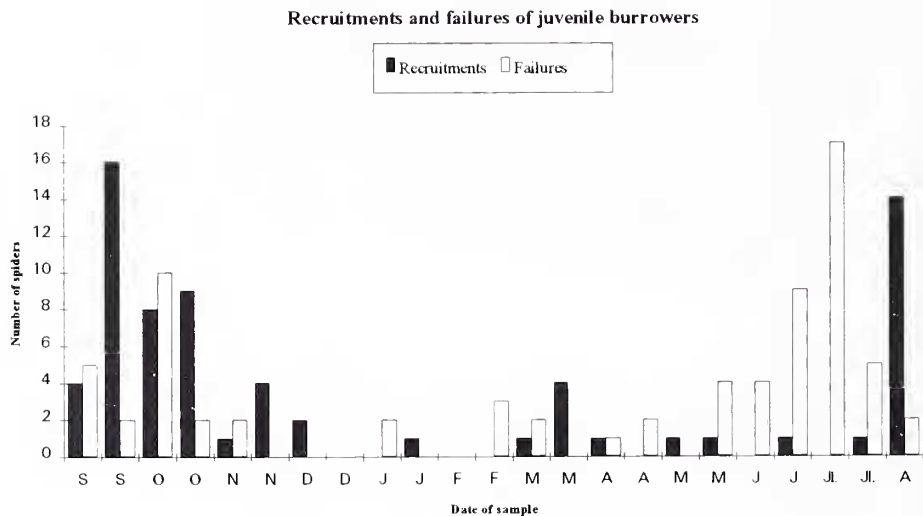


FIG. 3

Note that the number of juveniles that left their burrows during September–October, never is larger than the number of new settlers before winter. Two peaks of burrow settlement are clear (September and August).



### Nearest Neighbour Distance

The results of the nearest neighbour analysis for each sampling date are shown in table I. The dates corresponding with early and mid July have been discarded because males left their burrows looking for females. Due to a new settlement of burrows in early August, this sample has been analysed (fig. 3). Although sampling dates are not statistically independent, individuals are evenly distributed within the available area during almost the whole year.

Date	n	$r_a$	R	C	p
A	11	2.38	1.2	1.27	N S
S	12	2.74	1.44	2.92	0.025*
S	24	1.68	1.25	2.38	0.025*
O	26	1.44	1.11	1.1	N S
O	31	1.41	1.19	2.04	0.025*
N	31	1.56	1.32	3.42	0.001**
N	33	1.46	1.28	3.11	0.001**
D	34	1.45	1.29	3.18	0.001**
D	34	1.45	1.29	3.18	0.001**
J	33	1.41	1.23	2.51	0.025*
J	34	1.37	1.21	2.35	0.025*
F	34	1.37	1.21	2.35	0.025*
F	31	1.3	1.1	1.06	N S
M	31	1.37	1.16	1.68	N S
M	35	1.42	1.27	3.1	0.005*
A	34	1.53	1.35	3.93	0.0001***
A	33	1.5	1.31	3.41	0.001**
M	33	1.47	1.29	3.15	0.001**
M	30	1.61	1.34	3.56	0.001**
J	28	1.45	1.17	1.67	N S
J	23	1.61	1.18	1.62	N S
II	-	-	-	-	-
II	-	-	-	-	-
A	18	1.98	1.28	2.27	0.025*

TABLE I

Results of the nearest neighbour analysis in each sample date within the available area (white in fig. 1). The samples are not independent of each other. If  $R > 1$  and  $p < 0.05$  the spatial distribution is significantly regular. There is a trend towards a regular distribution across the samples.

## DISCUSSION

The two periods of juvenile maximum recruitment into the burrows can be explained by a lack of competition. In September, the spiderlings have already hatched, and the females may have allowed the juveniles to install themselves in their burrows, since they had a lower energy demand due to the end of the yolking period, and would have reduced their territorial behaviour. Until then, the juveniles would have survived in the population as floaters. The existence of floaters has been described in *Agelenopsis aperta* (Gertsch) (RIECHERT 1981). In August, the males had just abandoned their burrows searching for females, creating new areas with no competition, that would be used by floaters to establish their burrows. What happens between August and September has not been studied, but we can expect an important reduction in the number of established animals to occur. This would be the result of competition with females during this period, when they are yolking eggs and need a high rate of food intake. Other authors (FERNANDEZ-MONTRAVETA *et al.* 1991) have suggested that in this period, the spatial structure of the population is determined by females. This would support the hypothesis that competition increases during the time that females are building up stores for eggs.

The rest of the year, the burrow number did not change, presumably because the disappearances coincided with new recruitments. This suggests that what happened was a burrow relocation by the animals that left their previous one. Unfortunately, we have only observed two marked juveniles that had changed their burrows. The rest of recruitments observed during the year, of course, could be explained by animals that had changed their burrow and moulted simultaneously. In periods when this recruitment and failure pattern appears repeatedly (mainly in October), it would be convenient to carry out a more exhaustive monitoring to follow the recruitment and failure more closely. According to the model, the probability that a spider leaves its burrow, when it has not done so before, depends on its potential territory size and its relative size with respect to its neighbours' size. This could be evidence of density-dependent burrow leaving and thus of interference competition. The existence of floaters, demonstrated in an indirect way during the observation of the recruitment periods, seems to indicate that the burrow-sites are a limited resource in our population. The analyses of the nearest neighbour distances show that the spiders keep a regular distribution, that could be an indication of the existence of territoriality (DAVIES 1978). We can conclude that in this population, the role of interference competition on the numbers of juvenile burrowers could be important. Thus, burrowing wolf spiders appear to be an important source for investigating the Competitionist Paradigm in wandering spiders. Future research for improving this model is needed.

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## REFERENCES

- BARRIENTOS, J.A., MOYA-LARAÑO, J. & ORTA-OCAÑA, J.M. 1994. Algunes preferències de les taràntules a l'hora d'ubicar el cau. *L'entorn natural* 9: 14–19.
- BURGESS, J.W. & UETZ, G.W. 1982. Social spacing strategies in spiders, pp. 317–351. In: Spider Communitation: Mechanisms and Ecological Significance (P.N. WITT & J.S. ROVNER eds). *Princeton University Press, Princeton*, 440 pp.
- CLARK, P.J. & EVANS, F.C. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35(4): 445–453.
- COX, D.R. 1972. Regression Models and Life-Tables. *Journal of the Royal Statistical Society (London), series B*, 26: 103–110.
- DAVIES, N.B. 1978. Ecological Questions about Territorial Behaviour, pp. 317–350. In: Behavioural Ecology, an evolutionary approach (J.R. KREBS & N.B. DAVIES eds). *Blackwell Scientific Publications, Oxford*, 494 pp.
- DIGGLE, P.J. 1983. Statistical analysis of spatial point patterns, *Academic Press, Sydney*, 148 pp.
- DONCASTER, C.P. & WOODROFFE, R. 1993. Den site can determine shape and size of badger territories: implications for group-living. *Oikos* 66: 88–93.
- FERNANDEZ-MONTRAVETA, C., LAHOZ-BELTRA, R. & ORTEGA, J. 1991. Spatial Distribution of *Lycosa tarentula fasciiventris* (Araneae, Lycosidae) in a population from Central Spain. *Journal of Arachnology* 19: 73–79.
- KENKEL, N.C., HOSKINS, J.A. & HOSKINS, W.D. 1989. Edge effects in the use of area polygons to study competition. *Ecology* 70(1): 272–274.
- MCQUEEN, D.J. 1978. Field studies of growth, reproduction, and mortality in the burrowing wolf spider *Geolycosa domifex* (Hancock). *Canadian Journal of Zoology* 56: 2037–2049.
- MUENCHOW, G. 1986. Ecological use of failure time analysis. *Ecology* 67(1): 246–250.
- ORTA, J.M., MOYA, J. & BARRIENTOS, J.A. 1993. Datos fenológicos de una población de *Lycosa tarentula fasciiventris* L. Dufour, 1835, en el Noreste de la Península Iberica (Araneae, Lycosidae). *Bolletino dell' Accademia Gioenia di Scienze Naturali* 26(345): 15–26.
- RIECHERT, S.E. 1981. The consequences of being territorial: spiders, a case study. *The American Naturalist* 117(6): 871–892.
- RIECHERT, S.E. 1982. Spider Interaction Strategies: Communication vs. Coercion, pp. 281–315. In: Spider Communication: Mechanisms and Ecological Significance (P.N. WITT & J.S. ROVNER eds). *Princeton University Press, Princeton*, 440 pp.
- SINCLAIR, D.F. 1985. On tests of spatial randomness using mean nearest neighbor distance. *Ecology* 66(3): 1084–1085.
- WISE, D.H. 1993. Spiders in Ecological Webs. *Cambridge University Press, Cambridge*, 328 pp.
- WISE, D.H. & WAGNER, J.D. 1992. Evidence of exploitative competition among young stages of the wolf spider *Schizocosa ocreata*. *Oecologia (Berlin)* 91: 7–13.